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Original Investigation

Winter foraging activity of Central European Vespertilionid bats

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ABSTRACT

The winter activity of bats was studied in an area of Bavaria, Southern Germany, for seven consecutive years (2007–2013). Echolocation calls were recorded in known foraging areas between October and March of each winter, and bats were regularly seen on evenings with temperatures above +6 °C, except for the period between mid-December and mid-February, when even bouts of warm weather did not appear to trigger foraging activity. Below +3 °C no bats appeared in the foraging areas. The most frequently recorded species were *Nyctalus noctula*, *Pipistrellus pipistrellus*, *Pipistrellus nathusii* and *Vespertilio murinus*. Final buzzes indicating attempts to catch prey were recorded for these species even in December and February, which supports the idea that the bats were not only in search of water or just moving between roosts. *Myotis* species, on the other hand, which hibernate in roosts offering more constant temperature conditions, were not observed at all between mid-November and March. Further investigations have to show whether warmer winter evenings offer bats an opportunity for casual hunting or whether winter foraging expresses an urgent need for weak individuals.

Introduction

Bats of northern latitudes are known to hibernate in winter and many studies have described conditions and duration of hibernation including arousals and flight activity at the roosts (e.g. Berkova et al., 2002; Daan, 1973; Furmankiewicz and Gorniak, 2002; Hope and Jones, 2012; Johnson et al., 1998; Parsons et al., 2003; Thomas, 1995a,b; Wermundsen and Siivonen, 2010). However, individuals of some bats species are regularly found outside roosts during winter. Often such observations occur because bats move between roosts potentially due to changes of roost climate or disturbances (Sendor et al., 2000). Other reasons for their activity might be dehydration and foraging (Geluso, 2007; Lausen and Barclay, 2006; Speakman and Racey, 1989; Whitaker and Rissler, 1992, 1993) and also mating (Johnson et al. 2012). In North America, winter feeding has been shown at least for some species (Dunbar et al., 2007) and in Western and Southern Europe, where winters are milder, foraging activity occurs regularly (Avery, 1985, 1986; Hays et al. 1991; Park et al., 1999, 2000; Ransome, 2002; Rodrigues et al., 2003). In Central Europe with its long periods below 0 °C, species such as *Pipistrellus nathusii* and *Vespertilio murinus* often fly into houses in late autumn and winter or are found in an exhausted state, probably due to the search for adequate roosts (Liegl, 2004; Meschede, 2004). Noctules (*Nyctalus noctula*) from hibernation colonies swarm close to their roosts on most winter days (Zahn and Clauss, 2003). However, observations of bats in foraging areas during winter are rare in Central Europe. Bat foraging activity is related to climate, especially temperature. Below 8 °C foraging bats are rarely recorded (Zahn and Maier, 1997). Temperatures are lower than this on most winter evenings in Central Europe, presumably preventing the search for food. Nevertheless, warmer nights can occur even in the coldest of months providing bats the opportunity for hunting. It is known that some insects are active in this season (Ressl 1967), and one can expect that bats of low weight interrupt hibernation and try to forage to lower the risk of starvation.

Unfortunately, systematic studies on bat activity in foraging areas during Central European winters are lacking. Therefore it is not known, whether and how frequent winter foraging currently occurs, which makes it impossible to monitor a possible behavioural change of bats as a consequence of a warming climate in the future.

This study therefore focuses on foraging activity in winter in a current study area north of the Bavarian Alps, considering temperature, insect activity and the course of the season. It can be hypothesized that temperature and food abundance influence bat activity during winter and that foraging activity concentrates at sites which offer comparatively abundant food as for example non-frozen rapid flowing rivers. Further it can be expected, that bats species which hibernate in thermally stable underground roosts (e.g. *Myotis*—species) are less active in winter than those species

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which roost in tree-holes or crevices on the outside of buildings where roost temperatures are strongly influenced by ambient temperature.

Material and methods

The winter activity of bats between October and March was studied in Southeastern Bavaria, Southern Germany, for seven consecutive years (2007/08–2012/13) on 116 evenings (Table 1). Most data were obtained at the banks of the river Inn at Waldkraiburg (N48°11′, E12°24′, 66 samples) and in adjoining woodlands, a spruce forest edge (N48°12′, E12°23′; 16 samples) and a deciduous forest edge (N48°10′, E12°23′ 13 samples). Single observations were made at rivers Traun (N47°55′, E12°37′; 5 samples) Mangfall (N47°53′, E11°52′, 8 samples) and Salzach (N47°56′, E12°56′, 8 samples). All the sites were known to be foraging areas of several species during summer or autumn according to unpublished preliminary studies. The bat fauna of the study area is well known (Meschede and Rudolph 2010).

Frequent species consist of *Plecotus auritus, Myotis daubentonii, Myotis mystacinus, Myotis brandtii, Myotis myotis* and *Myotis nattereri, Pipistrellus pipistrellus, Pipistrellus nathusii, Nyctalus noctula* and *Vespertilio murinus.* Species which occur only infrequently in the study area are *Barbastella barbastellus, Eptesicus nilssonii, Eptesicus serotinus, Hypsugo savii, Nyctalus leisleri, Myotis bechsteinii* and *Pipistrellus pygmaeus*.

The echolocation calls were recorded at the sample sites with a Pettersson D1000 bat detector and a batcorder (ecoObs GmbH, type 2.0; instrument adjustment: threshold −36 dB, quality 20). Samples were taken for 30–60 min starting 15 min after sunset and the activity calculated on a 5 min base (records/5 min). Using the D1000, as many records as possible during a study section were made. The batcorder recorded sound samples automatically but a comparison verified that similar numbers of records were obtained with both methods. The records were analysed automatically by the program bcAnalyze 2.0 (ecoObs GmbH,) and verified using batsound software 3.31 (Pettersson,). Additionally we measured the total bat activity (seconds/5 min) and estimated the number of feeding buzzes that could be recorded by the bat detector. Half-way through each sample-taking the air temperature was measured with a conventional digital thermometer. The availability of prey was assessed during sampling with the help of a flashlight by counting the number of insects visible in a standardised flashlight beam during a slow full turn (Taylor and O'Neill, 1988). After five repeats the mean number of insects was calculated.

During sound analysis, many records could not be determined to species level. The species *Vespertilio murinus, Eptesicus serotinus* and *Nyctalus leisleri* were pooled (group "Nyctaloid") following the batIdent software. The genus *Myotis* was treated as a group. However, visual observations indicate, that most samples belong to *Myotis daubentonii*. Further, it was not possible to clearly distinguish between *Pipistrellus nathusii* and *Pipistrellus kuhlii*. According to social calls and many random records of bats found during the study period, only *Pipistrellus nathusii* occurs in the area, although the situation may change in future due to the range expansion of *Pipistrellus kuhlii* in Bavaria (Rudolph et al. 2010).

In *Pipistrellus pygmaeus*, *Eptesicus nilssonii*, *Hypsugo savii*, *Barbastella barbastellus and the* genus *Myotis* we could only state whether or not a species was present on a given evening without quantifying the activity. In these cases we gave the percentage of evenings during which a species could be observed. Only in *Pipistrellus nathusii, Pipistrellus pipistrellus, Nyctalus noctula* and "Nyctaloids" we were able to conduct a quantitative analyses of foraging activity.

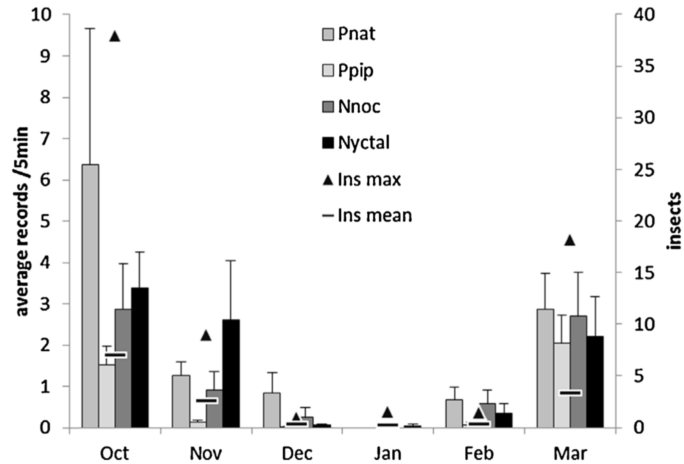

Fig. 1. Activity of *Pipistrellus nathusii* (Pnat), *Pipistrellus pipistrellus* (Ppip), *Nyctalus noctula* (Nnoc), and "Nyctaloids" (Nyctal) at the rivers during seven winters. Given are the average numbers of records in a 5-min-period and the standard error. "Ins mean" refers to the average number of insects and "Ins max" to the maximum number of insects counted in the given month.

Since the data were not normally distributed, Spearman's rho correlation coefficient (nonparametric) was used to analyse the strength of association between the bat activity and the factors temperature (activity against temperature) and insect abundance (activity against insect abundance). To counteract the problem of multiple comparisons, the Holm–Bonferroni correction method was used.

Results

Bat activity at rivers occurred throughout the whole winter but between mid-December and mid-February records were rare even on warm evenings. The most often recorded species were *Pipistrellus nathusii*, *Pipistrellus pipistrellus*, *Nyctalus noctula* and "Nyctaloids", with *Vespertilio murinus* being probably dominant in the latter group. Rarer species were *Pipistrellus pygmaeus, Eptesicus nilssonii, Hypsugo savii, Barbastella barbastellus* and *Myotis spec* (Table 1). In January only two observations were made: A *Vespertilio murinus* was foraging at 7.4 °C with a final buzz audible and a single call of *Pipistrellus nathusii* was recorded at 14.2 °C in spite of severe wind.

Throughout winter, feeding buzzes were recorded in all the bat species present in a given month, thus indicating frequent foraging attempts. In November high numbers of feeding buzzes could be heard regularly and even in the first week of December a *Barbastella barbastellus* was observed patrolling along a woodland edge searching for food. Between mid-December and mid-February buzzes were heard on three of seven evenings with bat activity. In one of these cases a Nyctaloid bat (probably *Vespertilio murinus*) emitted 19 feeding buzzes within a few minutes in late December. From late February onwards buzzes were frequent again in pipistrelles and noctules.

Fig. 1 gives the average activity of the most abundant bat species during winter. *Pipistrellus nathusii*, *Nyctalus noctula* and "Nyctaloids" showed a high activity at the beginning of the hibernation period while in *Pipistrellus pipistrellus* it was more pronounced at the end. The lowest temperature at which foraging activity could be observed was 3.0 °C and above 6 °C several species foraged regularly (Fig. 2). During the main hibernation period between November and February, a distinct correlation (Table 2) was determined between activity in all the species and both insect abundance ($p < 0.05$) and temperature ($p < 0.05$). Insect abundance and temperature were also closely correlated ($p < 0.05$)). Except in *Pipistrellus*

Table 1
Presence of bat species in foraging areas during seven winters. Given is the percentage of all evenings (n) in the study period on which a species could be verified. Pnat = *Pipistrellus nathusii*, Ppip = *Pipistrellus pipistrellus*, Ppyg = *Pipistrellus pygmaeus*, Nnoc = *Nyctalus noctula*, Nyctal = "Nyctaloids", Enil = *Eptesicus nilssonii*, Hsav = *Hypsugo savii*, Bbar = *Barbastella barbastellus*, Myo = genus *Myotis*. Ins = percentage of evenings (N) with insect activity. T-min is the minimum temperature (°C) at which a species could be observed.

	n	Pnat	Ppip	Ppyg	Nnoc	Nyctal	Enil	Hsav	Bbar	Myo	Ins
Oct	20	94.4	85.0	30.0	78.9	70.0	20.0	0.0	15.0	40.0	92.9
Nov	27	48.1	29.6	3.7	51.9	33.3	11.5	0.0	18.5	7.4	82.6
Dec	16	31.3	18.8	0.0	12.5	31.3	0.0	0.0	6.3	0.0	26.7
Jan	14	7.1	0.0	0.0	0.0	7.1	0.0	0.0	0.0	0.0	14.3
Feb	20	55.0	15.0	5.0	40.0	20.0	0.0	0.0	0.0	0.0	21.1
Mar	19	88.9	73.7	31.6	38.9	57.9	15.8	21.1	10.5	15.8	62.5
T-min		3.1	3.5	4.5	3.1	4.1	5.8	9.1	3.0	3.5	2.8

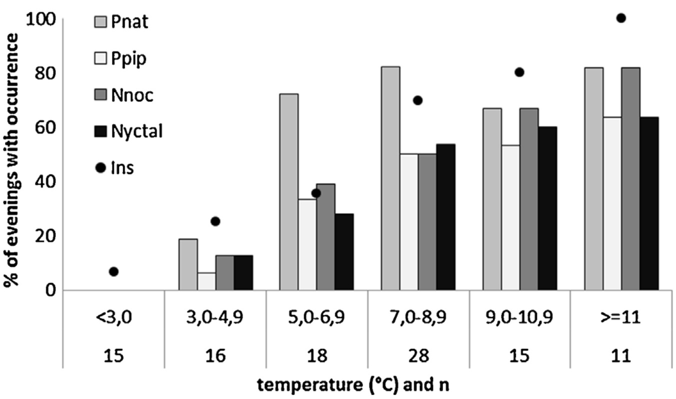

Fig. 2. Activity of *Pipistrellus nathusii* (Pnat), *Pipistrellus pipistrellus* (Ppip), *Nyctalus noctula* (Nnoc), and "Nyctaloids" (Nyctal) at different temperatures. n: number of samples in the given temperature range over the entire study period. For every temperature range, the percentage of evenings, on which the presence of a species or insects (Ins) could be verified, is given.

pipistrellus, the correlation between activity and temperature was stronger than between activity and insect abundance. However, higher temperatures did not automatically trigger bat activity. Especially between mid-November and February on many evenings with temperatures above 6 °C no bats were observed (Fig. 3). Activity occurred mainly on evenings after sunny days, especially at the first warm day after cold periods.

The activity in forests was much lower than at the rivers, even if only warm evenings are considered. On five evenings between 26/10 and 07/12, when the activity was recorded at the edge of a spruce forest (temperatures 4.0 °C, 8.0 °C, 8.1 °C, 9.0 °C and 7.5 °C) only between 0.2 and 0.5 records/5 min of the species *Pipistrellus nathusii, Nyctalus noctula, Eptesicus nilssonii, Barbastella barbastellus* and the genus *Myotis* were obtained. Each species was present only on one or two of the evenings. On six warm evenings between 27.10. and 29.11 (evening temperatures 8.9 °C, 13.5 °C, 12.1 °C, 8.1 °C, 4.1 °C and 5.8 °C) activity was also low in the deciduous forest and at its edge. Between 0.2 and 1.8 records/5 min of the species *Pipistrellus nathusii, Pipistrellus pipistrellus*, *Nyctalus noctula*, "Nyctaloids", *Barbastella barbastellus* and the genus *Myotis* were taken. At the rivers, much higher activities occurred at that time. After 07/12 no bat was heard during 6 sample sections in the forests until the end of February when single sequences of *Pipistrellus nathusii* and *Nyctalus noctula* were recorded at the edge of the spruce forest.

Table 2
Relation between bat activity and the factors temperature and insect abundance based on samples taken from November until February (n = 73). Given is Spearman's rho correlation coefficient. All correlations are significant (p < 0.05) after Holm–Bonferroni correction. Pnat = *Pipistrellus nathusii*, Ppip = *Pipistrellus pipistrellus*, Nnoc = *Nyctalus noctula*, Nyctal = "Nyctaloids".

	Pnat	Ppip	Nnoc	Nyctal	Insects
Temperature (°C)	0.438	0.286	0.469	0.356	0.515
Insects	0.294	0.326	0.304	0.278	

Remarkably, prior to the first period of severe frost in December, big moths were frequently observed in the forests, proving that food was available there. The mean number of insects measured at those evenings was 2.8 in the spruce forest and 3.5 in the deciduous forest. At the rivers the value was only 2.1 insects on evenings with temperatures above 4 °C during the same period.

Discussion

According to the observations in Southern Bavaria, some bat species forage regularly in winter with activity concentrated at sites known as good foraging areas like water bodies. Admittedly, between November and February the activity is much lower than in the month before or after that period and during mid-winter bats in foraging areas are very rare, even on warm evenings. However, until December and from late February onwards, bouts of higher activity occur repeatedly. A very similar pattern was observed by Avery (1985) in Great Britain. He found pipistrelles foraging in every winter month except February, with a lower activity in mid-winter compared to early or late winter.

The species which were observed foraging most often in Bavaria belong to the genera *Pipistrellus, Nyctalus* and the group "Nyctaloids" whereby the results of the automatic species discrimination by batIdent and the manual verification suggested that the vast majority of Nyctaloid-records originate from *Vespertilio murinus* which is in accordance with the abundance of the species in the area. All those bat species usually hibernate in roosts of varying temperatures, e.g. crevices in buildings, entrances of underground roosts or roosts in trees (Liegl, 2004; Meschede, 2004; Sachteleben et al., 2004; Zahn et al., 2004). In such shelters it might be easy for them to monitor ambient temperature and to sense good conditions for foraging. Additionally, on sunny days passive re-warming (Turbill and Geiser, 2008) of individuals roosting behind thin south-facing panels in shallow cavities may occur, which reduces the energy expenditure necessary for arousal. Zahn et al. (2000) measured up to 20 °C in sun exposed hibernation roosts of *Nyctalus noctula*. On the other hand, the low temperatures during frosty days in these roosts (as low as −10 °C), may cause a high energy loss during cold periods and many dead noctules can be found in those roosts after cold winters (Zahn, pers. observation). This makes foraging attempts worthwhile, if good conditions suddenly appear. Indeed, droppings under *Nyctalus noctula* roosts indicate foraging in winter (Kanuch et al., 2005). Noctules left their shelter regularly on the evenings of sunny days warmer than 7 °C and temperatures at dusk over 5.5 °C (Zahn and Clauss, 2003). Rudolph et al. (2010) also reported considerable flight activity during winter at Bavarian colony roosts of *Pipistrellus kuhlii*. In the mild winter 2013/2014 this species was foraging together with *Pipistrellus nathusii*, *Pipistrellus pygmaeus* and

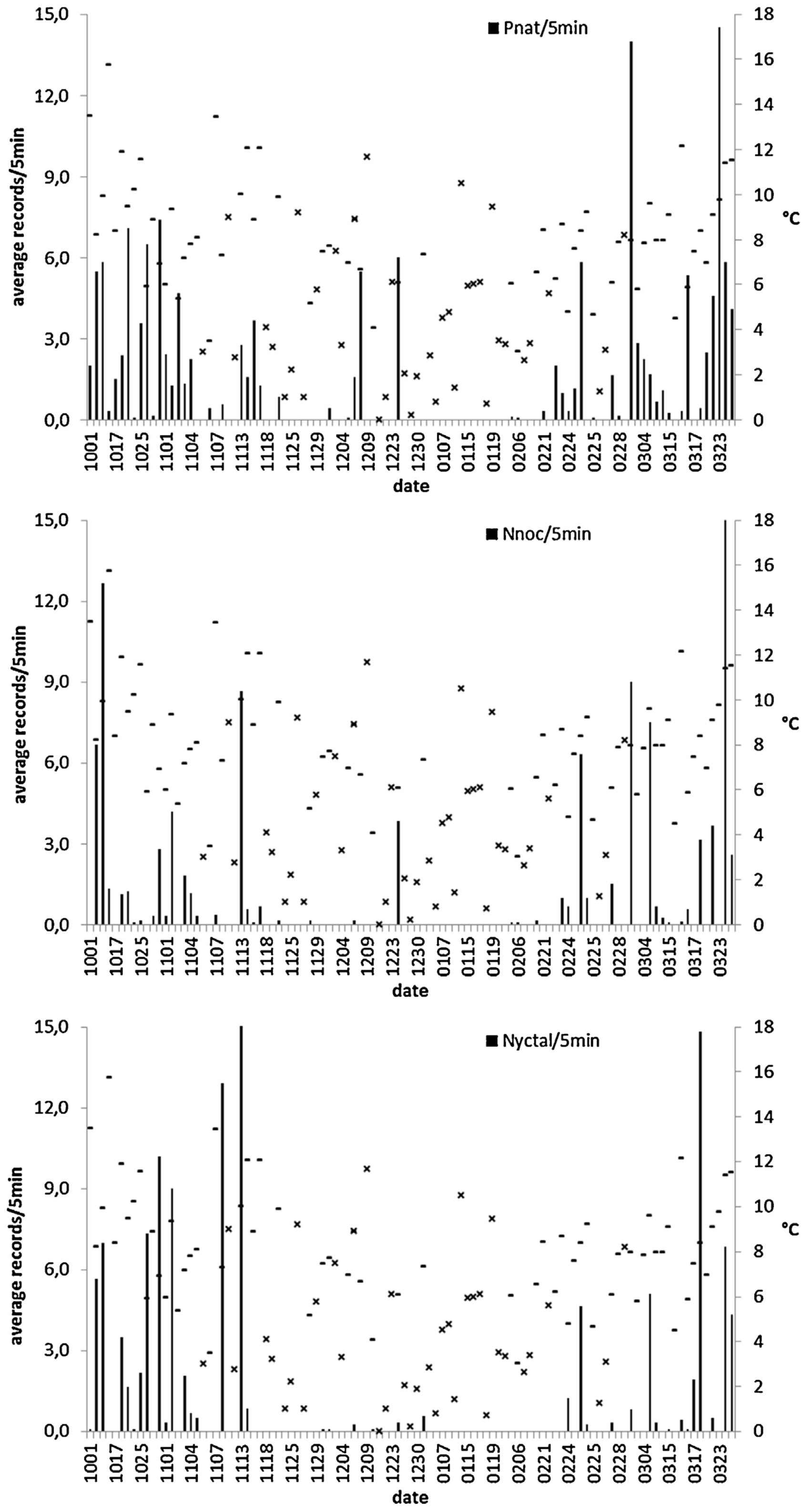

Fig. 3. Evening temperature and activity of the frequent species *Pipistrellus nathusii* (Pnat), *Nyctalus noctula* (Nnoc), and "Nyctaloids" (Nyctal). Given are the average numbers of records in a 5 min period. *x*/– = Temperature on evenings without and with bat activity (of any species).

Pipistrellus pipistrellus over a river in Augsburg on several evenings between early January and mid-February (Rudolph, pers. communication).

On the contrary, *Myotis* species, hibernating in roosts of constant temperature as caves or cellars (Meschede and Rudolph, 2004), were not active in foraging areas during winter. In general, cave-dwelling bats tend to be relatively inactive (Speakman and Racey, 1989).

However, there are only few hibernation roosts of these species known in the study area (Meschede and Rudolph 2010) and therefore it might be that the lack of activity is also caused by seasonal emigration of the bats. Hope and Jones (2012), for example, found a

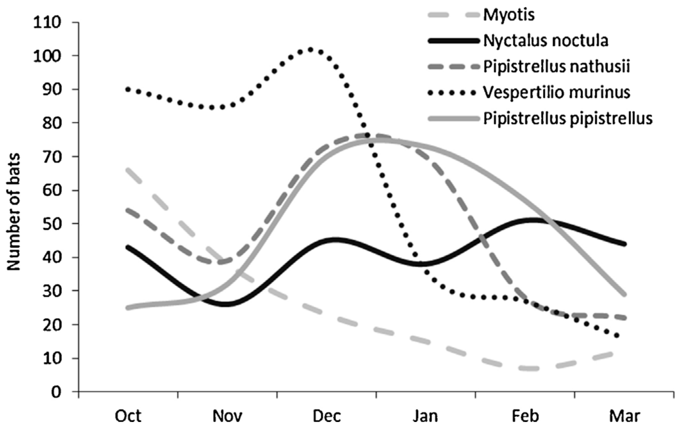

Fig. 4. Frequency of accidental findings (registered from 1980–2010 by the Coordination Office for Bat Conservation (Meschede and Rudolph 2010) in Southern Bavaria during winter. Given are the total numbers of individuals per month over a period of 30 years. Myotis = *Myotis species*.

considerable amount of activity in *Myotis nattereri* in winter, albeit in a location with a maritime climate. The authors believe, that the bats time their arousals to maximise opportunities for potential foraging. That *Myotis* species may in fact do display foraging behaviour in winter is additionally supported by studies in southern Europe, for example in case of the Greater Mouse-eared Bat (*Myotis myotis*, Rodrigues et al., 2003). However, due to the higher temperatures in Mediterranean underground roosts, hibernation patters were generally different.

Interestingly, *Barbastella barbastellus*, which hibernates in underground roosts too, could be observed foraging in the study area as late as December. It is known, that this species is present in underground roosts mainly during the coldest periods in winter and that many individuals leave those roosts as soon as temperatures start to rise (Rudolph, 2004). Hirschfelder (personal communication) recorded *Barbastella barbastellus* flying at the river Danube (Bavaria) as early as 28 February. Additionally he observed a *Plecotus austriacus* appearing at a night roost in the town of Kelheim daily between 2/11/08 and 14/11/08. This also indicates winter foraging activity of a bat species hibernating in underground roosts.

The phenology of bat activity in foraging areas differs considerably from the occurrence of accidental findings (bats found exhausted outside roosts or individuals that fly into houses) during winter (Fig. 4). High numbers of *Nyctalus noctula*, *Pipistrellus nathusii*, *Pipistrellus pipistrellus* and *Vespertilio murinus* are registered in December and January, the period of the lowest foraging activity. Probably this pattern reflects roost changes during winter and has nothing to do with the activity in foraging areas. Nevertheless, a common reason for both behaviours is probably the usage of poorly sheltered hibernation roosts as mentioned above. The use of multiple sites for hibernation and the foraging attempts may be necessary to compensate for the lack of environmentally stable roost conditions (Speakman and Racey, 1989). This is supported by the differing phenology of the genus *Myotis* (Table 1, Fig. 4), which hibernates mostly in well sheltered places.

However, as of now it remains unknown whether winter foraging expresses an urgent need for nourishment due to unfavourable roost conditions or whether some bats behave opportunistically and put on additional food. This question is particularly interesting considering the expected alteration of winter temperatures due to climate change. The presented data can serve as a baseline in determining behavioural modifications caused by warmer winter seasons in Central Europe among the studied bat species.

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References

Avery, M.I., 1985. Winter activity of pipistrelle bats. J. Anim. Ecol. 54, 721–773.
Avery, M.I., 1986. The winter activity of noctule bats (*Nyctalus noctula*). J. Zool. 209, 296–299.
Berkova, H., Zukal, J., Rehak, Z., 2002. Flight activity of bats at the entrance of a natural cave. Bat Res. News 43, 76.
Daan, S., 1973. Activity during natural hibernation in three species of vespertilionid bats. Neth. J. Zool. 23, 1–71.
Dunbar, M.B., Whitaker, J.O., Robbins, L.W., 2007. Winter feeding by bats in Missouri. Acta Chiropterologica 9 (1), 305–322.
Furmankiewicz, J., Gorniak, J., 2002. Seasonal changes in number and diversity of bat species (Chiroptera) in the Stolec mine (SW Poland). Przyr. Sud. Zach., Suppl. 2, 49–70.
Geluso, K., 2007. Winter activity of bats over water and along flyways in New Mexico. Southwestern Nat. 52 (4), 482–492.
Hays, G.C., Speakman, J.R., Webb, P.I., 1991. Why do brown long-eared bats (*Plecotus auritus*) fly in winter? Physiol. Zool. 65, 554–567.
Hope, P.R., Jones, G., 2012. Warming up for dinner: torpor and arousal in hibernating Natterer's bats (Myotis nattereri) studied by radio telemetry. Journal of Comparative Physiology B 182, 569–578.
Johnson, J.S., Lacki, M.J., Thomas, S.C., Grider, J.F., 2012. Frequent arousals from winter torpor in Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). PLoS One 7 (11), e49754, http://dx.doi.org/10.1371/journal.pone.0049754.
Johnson, S.A., Brack, V., Rolley, R.E., 1998. Overwinter weight loss of Indiana bats (*Myotis sodalis*) from Hibernacula subject to human visitation. Am. Midland Nat. 139, 255–261.
Kanuch, P., Janeckova, K., Kristin, A., 2005. Winter diet of the noctule bat *Nyctalus noctula*. Folia Zoologica 54 (1–2), 53–60.
Lausen, C.L., Barclay, R.M.R., 2006. Winter bat activity in the Canadian prairies. Can. J. Zool. 84, 1079–1086.
Liegl, C., 2004. Zweifarbfledermaus *Vespertilio murinus*. In: Meschede, A., Rudolph, B.U. (Eds.), Fledermäuse in Bayern. Ulmer Verlag, Stuttgart, pp. 296–304.
Meschede, A., Rudolph, B.U., 2004. Landesweite Auswertungen. In: Meschede, A., Rudolph, B.U. (Eds.), Fledermäuse in Bayern. Ulmer Verlag, Stuttgart, pp. 58–96.
Meschede, A., 2004. Rauhautfledermaus *Pipistrellus nathusii*. In: Meschede, A., Rudolph, B.U. (Eds.), Fledermäuse in Bayern. Ulmer Verlag, Stuttgart, pp. 280–290.
Meschede, A., Rudolph, B.U., 2010. 1985–2009: 25 Jahre Fledermausmonitoring in Bayern. Schriftenr. des Bayerischen Landesamtes für Umwelt. Bayerisches Landesamt für Umweltschutz, Augsburg.
Park, K.J., Jones, G., Ransome, R.D., 2000. Torpor, arousal and activity of hibernating greater horseshoe bats. Funct. Ecol. 14, 580–588.
Park, K.J., Jones, G., Ransome, R.D., 1999. Winter activity of a population of greater horseshoe bats (*Rhinolophus ferrumequinum*). J. Zool. Lond. 248, 419–427.
Parsons, K.N., Jones, G., Greenaway, F., 2003. Swarming activity of temperate zone microchiropteran bats: effects of season, time of night and weather conditions. J. Zool. 261, 257–264.
Ransome, R.D., 2002. Winter feeding studies on greater horseshoe bats. In: English Nature Research Reports No. 449. English Nature, Peterborough, pp. 1–47.
Ressl, F., 1967. Über das Vorkommen einiger winteraktiver Insekten im Bezirk Scheibbs (N.Ö.). Entomologisches Nachrichtenblatt 14, 85–87.
Rodrigues, L., Zahn, A., Rainho, A., Palmeirim, J., 2003. Contrasting the roosting behaviour and phenology of an insectivorous bat (*Myotis myotis*) in its southern and northern distribution ranges. Mammalia 67, 321–335.
Rudolph, B.U., 2004. Mopsfledermaus *Barbastella barbastellus*. In: Meschede, A., Rudolph, B.U. (Eds.), Fledermäuse in Bayern. Ulmer Verlag, Stuttgart, pp. 340–355.
Rudolph, B.U., Lichti, H., Liegl, C., Pichl, S., 2010. Verbreitung, status und erste Erkenntnisse zum Verhalten und zur Ökologie der Weißrandfledermaus, *Pipistrellus kuhlii* (Kuhl, 1817), in Bayern. Nyctalus (N.F.) 15, 191–212.
Sachteleben, J., Rudolph, B.U., Meschede, A., 2004. Zwergfledermaus *Pipistrellus pipistrellus*. In: Meschede, A., Rudolph, B.U. (Eds.), Fledermäuse in Bayern. Ulmer Verlag, Stuttgart, pp. 263–275.
Sendor, T., Kugelschafter, K., Simon, M., 2000. Seasonal variation of activity patterns at a pipistrelle (*Pipistrellus pipistrellus*) hibernaculum. Myotis 38, 91–109.
Speakman, J.R., Racey, P.A., 1989. Hibernal ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. J. Anim. Ecol. 58, 797–813.
Taylor, R.J., O'Neill, M.G., 1988. Summer activity patterns of insectivorous bats and their prey in Tasmania. Aust. Wildl. Res. 15, 533–539.
Thomas, D.W., 1995a. The physiological ecology of hibernation in vespertilionid bats. Symp. Zool. Soc. Lond. 67, 233–244.
Thomas, D.W., 1995b. Hibernating bats are sensitive to non-tactilehuman disturbance. J. Mammal. 76, 940–946.
Turbill, C., Geiser, F., 2008. Hibernation by tree roosting bats. J. Comp. Physiol. B. 178, 597–605.

Wermundsen, T., Siivonen, Y., 2010. Seasonal variation in use of winter roosts by five bat species in south-east Finland. Cent. Eur. J. Biol. 5, 262–273.

Whitaker Jr., J.O., Rissler, L.J., 1992. Winter activity of bats at a mine entrance in Vermillion County, Indiana. Am. Midland Nat. 127, 152–159.

Whitaker Jr., J.O., Rissler, L.J., 1993. Do bats feed in winter? Am. Midland Nat. 129, 200–203.

Zahn, A., Clauss, B., 2003. Winteraktivität des Abendseglers (*Nyctalus noctula*) in Südbayern. Nyctalus (N.F.) 9 (2), 99–104.

Zahn, A., Maier, S., 1997. Jagdaktivität von Fledermäusen an Bächen und Teichen. Zeitschrift für Säugetierkunde 62, 1–11.

Zahn, A., Christoph, C., Christoph, L., Kredler, M., Reitmeier, A., Reitmeier, F., Schachenmeier, C., Schott, T., 2000. Die Nutzung von Spaltenquartieren an Gebäuden durch Abendsegler (*Nyctalus noctula*) in Südostbayern. Myotis 37, 61–76.

Zahn, A., Meschede, A., Rudolph, B.U., 2004. Abendsegler (*Nyctalus noctula*). In: Meschede, A., Rudolph, B.U. (Eds.), Fledermäuse in Bayern. Ulmer Verlag, Stuttgart, pp. 232–252.